

POLLINATION IN PIPERACEAE¹

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ABSTRACT

A study of four *Piper* species and one *Pothomorphe* species in Costa Rica showed that insects do visit some Piperaceae flowers and are probably involved in pollination. Due to the globular nature of the pollen it is not likely that wind or rain are significant pollination agents. The degree of self-pollination for the species studied has not been determined, although presumably some may occur because *Piper nigrum* has been found to be partially self-fertile.

The family Piperaceae is pantropical in distribution with *Piper nigrum* L., the source of black and white pepper, its best known representative. It has been thought that pollination in this family occurs by wind or rain because of the similarity of its minutely-flowered, spicate inflorescences to known wind-pollinated plants in the Amentiferae (Menon, 1949; Martin & Gregory, 1962). A pollination study of four *Piper* species and one *Pothomorphe* species in Costa Rica showed that insects as well as weather are involved in pollination in the Piperaceae.

The inflorescence characteristic of the Piperaceae may be described as a spike of closely packed minute flowers. Flowers of Costa Rican species are bisexual (Burger, 1971). Perianth parts are absent and a floral bract subtends each flower. The gynoecium is unilocular with one ovule and usually has a style with three to five stigmatic branches. There are four stamens, rarely two or six, attached to the base of the pistil. Anther filaments are short with bilobed anthers borne at the level of the stigmas (Burger, 1971). The fruit is drupaceous and fleshy or dry.

The flowers are protogynous, the stigmas being exerted several days before anther dehiscence. Anthesis proceeds from base to tip of a spike, taking about a week for all flowers to open (Menon, 1949). Pollen is held together in glutinous masses, parts of which are shed for up to five days after dehiscence. In *Piper nigrum* stigmas are exerted three to eight days ahead of anther dehiscence, and receptivity lasts for up to ten days. According to Martin and Gregory (1962), in spite of differences in sexual expression, it is possible for the pollen of any spike to fertilize the entire spike if properly distributed.

Although Gentry (1955) reported high fruit set in a dioecious clone of black pepper with no staminate flowers visible, experimental evidence and growing experience show poor fruit set in the absence of staminate flowers (Menon, 1949; Martin & Gregory, 1962). Therefore it is assumed that for good fruit set pollination rather than apomixis occurs. In India it has been the belief that the agent of pollination in *Piper nigrum*, at least, is the monsoon rains (Menon, 1949).

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Others have suggested that Piperaceae are wind-pollinated (Martin & Gregory, 1962), having small pollen, a feathery style, and many small flowers in spicate inflorescences. Martin and Gregory's paper (1962) is the only known previously published report of insects on Piperaceae inflorescences. In a study of *Piper nigrum* in Puerto Rico, spring tails (order Collembola) were commonly seen. Because of erratic fruit set they did not appear to be important in pollination and were more noted for disturbance and damage to the flowers and fruits. The conclusion is that the cultivated pepper is mostly self-pollinated with rain possibly increasing the efficiency of pollination. Previous unpublished Organization for Tropical Studies class reports have recorded bee and fly insect visitors on Piperaceae flowers (Hines, 1967; Weaver, 1968).

MATERIALS AND METHODS

Five sites, including four species of *Piper* and one *Pothomorphe*, were selected for the pollination study at the Tropical Science Center Field Station, Rincón de Osa, Costa Rica: three sites on the edges of primary forest and two sites in secondary growth areas. The Piperaceae species observed were *Piper aduncum* L., *P. auritum* H.B.K., *P. friedrichsthali* C. DC. in DC., *P. villiramulum* C.DC., and *Pothomorphe peltata* (L.) Miq. From 5–10 August 1971, each site was visited for a thirty-minute interval during the period of insect activity, from 6:00 to 9:30 a.m. Each site was visited at each time interval, allowing fifteen minutes to travel between sites. At each site twenty spikes were observed, the number for each species depending on its prevalence. The different pollinators were noted and the number of visits of each insect species was recorded during the half-hour interval.

Pollen was examined by scraping pollen off the bees' pollen baskets into a glassine envelope. In the lab pollen was transferred to a slide, stained with fuchsin glycerine jelly (Beattie, 1971), and examined under a microscope.

RESULTS

Observations showed that insects do visit inflorescences of the Piperaceae species studied. Several species of *Trigona* bees were the most common visitors, and several small Coleoptera were next most numerous (Table 1). The most common *Trigonas* were *Trigona dorsalis* Smith, *T. latitarsis* Friese, and *T. perangulata* Cockerell. Also observed were *T. mexicana subobscuripennis* Schwarz, *T. nigerrima* Cresson, and halictid bees of the genera *Augochloropsis* and *LasioGLOSSUM*. It appears that the *Trigona* bees do promote pollination, because they collect large amounts of pollen in their pollen baskets by working up and down the spikes collecting pollen, and they fly from spike to spike. Wind-pollination is unlikely because of the glutinous nature of the pollen. Pollen was present on the spikes for at least five days through numerous rain storms, indicating that it is not easily washed or blown away.

Trigonas did not differentiate among the Piperaceae species except that more than twice as many bees of each species visited *Piper auritum*. Perhaps *P. auritum* is preferred because it has longer spikes, from 12 to 30 cm long, and thus more pollen than the other species. Also it may be recognized by a distinctive "licorice-like" odor when the leaves are crushed.

Pollination activity appeared to be largely determined by weather conditions. The peak of activity, between 8:00 and 10:00 a.m., coincided with the period of greatest sunlight. Fewer bees were seen under cloudy conditions, and none were seen during rainfall, which usually started around noon. The first

TABLE 1. Periods of pollinator activity in Piperaceae during five days at Rincón de Osa, Costa Rica.

	Time of observation (a.m.)				
	6:00–6:30	6:45–7:15	7:30–8:00	8:15–8:45	9:00–9:30
Hymenoptera	Number of Visits				
<i>Trigona dorsalis</i>					
<i>T. latitarsis</i>	—	—	14	51	74
<i>T. perangulata</i>					
<i>T. mexicana</i>	—	—	12	2	17
<i>T. nigerrima</i>	—	—	6	9	15
<i>Augochloropsis</i>					
<i>Lasioglossum</i>	—	—	2	—	—
COLEOPTERA	2	9	17	40	15

bees appeared around 7:30 a.m. when most of the dew had evaporated. Up to six bees were observed on a spike at a time, moving up, down, and around the spike without seeming to follow any pattern. During activity peaks it was difficult to follow a single bee. However, bees were seen going from one *Piper* species to another, indicating no strong species constancy on single foraging trips.

The most common Coleoptera seen, but not identified, first became numerous at 6:45 a.m. and appeared throughout the observation period. These beetles seem to eat pollen and probably cause some pollination, although pollen does not stick well to their rather smooth bodies. The few halictid bees observed were not significant pollination vectors, but are of interest because they represent a potential source of pollinators.

Pollen samples from *Trigona* bees were examined with the aim of determining if the bees visit flowers other than those of the Piperaceae. The pollen consisted mainly of Piperaceae pollen, however scattered grains of non-Piperaceae pollen were also observed.

DISCUSSION AND CONCLUSIONS

The Piperales are one of the most primitive dicot groups, derived from and closely related to the Magnoliales (Takhtajan, 1969). In spite of the outward similarity of the *Piper* inflorescence to the wind-pollinated Amentiferae, the Amentiferae are thought to have evolved from quite different evolutionary lines. Because the Magnoliales are insect-pollinated, it does not seem unusual that a closely related group would also have insect pollinators.

The Piperaceae studied occur in a variety of secondary and edge communities subject to harsh environmental extremes. As colonizing species they have evolved a generalized reproductive strategy conducive to survival in uncertain environments. The strategy involves producing more flowers and fruits, with less energy needed for formation of each individual flower; hence, the loss of the perianth. The fruits are small and easily dispersed by wind or by falling to the ground.

Bats may also be important in dispersal, as indicated by studies showing that bats eat *Piper* fruit (Fleming, 1972). Because the flowers are not specialized, the agent of pollination does not visit the flower in a precise way, and there may be several types of pollinators, *i.e.* various species of small Hymenoptera, small Coleoptera, and probably Diptera. If pollinators are not available, there is evidence (Martin & Gregory, 1962) that self-fertilization may occur. In *Piper nigrum* self-fertilization yields good fruit and presumably self-fertilization may occur in other *Pipers* as well.

The protogyny of Piperaceae flowers encourages outcrossing, although the timing is not sufficiently different to prevent pollination of flowers on the same spike by each other (Martin & Gregory, 1962). If apomixis occurs, it is quite rare. In an embryological study by Kanta (1961) the ovules in 50 per cent of the ovaries of *Piper nigrum* collapsed due to lack of pollination, and only 10 per cent of all ovules developed healthy embryos, indicating high sterility. More research needs to be done to determine if this sterility is due to environmental or genetic factors and to determine if it occurs in other *Piper* species.

It is not known if self-pollination or outcrossing predominates in the family. P. A. Opler (personal communication) has suggested that *Trigonas* are especially adapted for the pollination of some self-compatible plant species. *Trigonas* may aid in distributing pollen within a single spike and occasionally in distributing pollen between plants. Studies have shown (Allard, 1965) that this combination of self-fertilization and occasional outcrossing is highly successful and characteristic of a large number of colonizing species. The genetic system allows for perpetuation of superior genotypes and the introduction of a low level of genetic variability important to long term survival.

LITERATURE CITED

- ALLARD, R. W. 1965. Genetic systems associated with colonizing ability in predominantly self-pollinated species. In H. G. Baker & G. L. Stebbins (editors), "The Genetics of Colonizing Species." Academic Press, New York.
- BEATTIE, A. J. 1971. A technique for the study of insect-borne pollen. Pan-Pacific Entomol. 47: 82.
- BURGER, W. 1971. Piperaceae. Fieldiana Bot. 35: 5-227.
- FLEMING, T. 1972. Ecology of bat-plant interactions in Costa Rica. Missouri Botanical Garden Systematics Symposium, October 20-21, 1972.
- GENTRY, H. S. 1955. Apomixis in black pepper and jojoba. Jour. Hered. 46: 8.
- HINES, D. M. 1967. Pollination biology in three species of *Piper*. Organization for Tropical Studies tropical biology class report.
- KANTA, K. 1961. Embryolessness in *Piper nigrum* L. Phytomorphology 11: 304-306.
- MARTIN, F. W. & L. E. GREGORY. 1962. Mode of pollination and factors affecting fruit set in *Piper nigrum* L. in Puerto Rico. Crop Sci. 2: 295-299.
- MENON, K. K. 1949. The survey of pollu and root diseases of pepper. Ind. Jour. Agric. Sci. 19: 89-136.
- TAKHTAJAN, A. 1969. Flowering Plants: Origin and Dispersal. Smithsonian Institution Press, Washington.
- WEAVER, R. E. 1968. Studies in the pollination of Piperaceae. Organization for Tropical Studies botany course report.